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Notes on stratigraphy and geographical distribution of placodonts

Abstract – The aim of this work is to discuss the stratigraphy and the geographical distribution of placodonts.

Riassunto – Note sulla stratigrafia e sulla distribuzione geografica dei placodonti. Vengono discusse la distribuzione stratigrafica e la distribuzione geografica dei rettili placodonti.

Key words: Placodontia, stratigraphy, geographical distribution.

Introduction

Placodonts are a group of marine reptiles whose representatives lived in the shallow waters of Tethys and of the European epicontinental seas during the Middle and Upper Triassic.

The body of these animals is stocky; it is not well specialized for the aquatic life; it is characterized by a skull with a single temporal fenestra and by a set of flattened teeth specialized for a durofagous diet. The upper teeth are supported by the premaxillary, maxillary and palatine bones, while in the jaw they are supported by the dentary.

Placodonts were first discovered in 1830 by Georg Münster, who found two badly preserved skulls and some isolated teeth coming from the Bavarian

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Muschelkalk. He ascribed these remains to an indefinite group of fishes. Agassiz (1833) thought placodonts to be pycnodonts fishes. It was only in 1859 that they were ascribed to reptiles by Richard Owen, who also pointed out some affinities with the nothosaurs and plesiosaurs. Placodonts went unstudied for many years: some skulls and isolated teeth were ascribed to the two genera *Placodus* and *Cyamodus,* already identified by von Meyer in 1863. In 1901, the discovery of a complete skull in the hungarian Lower Keuper together with the remains of the postcranial skeleton and fragments of dermal armour (*Placochelys placodonta*), allowed Jaekel to recognize the existence of armoured placodonts and to ascribe to them some armour that was, until that moment, very difficult to interpret (*Psephoderma alpinum, Psephosaurus suevicus*). In 1915, Drevermann discovered an almost complete skeleton of *Placodus* in the Upper Muschelkalk, near Heidelberg. Additional placodont skeletons were found around 1930 by Peyer in Monte San Giorgio (*Paraplacodus broilii* and *Cyamodus hildegardis*). In 1934 some complete skeletons of a very peculiar placodont, *Henodus chelyops,* were brought to light from the Gipskeuper near Tübingen.

These findings allowed Huene (1936) to state that the order Placodontia included at least two different families: the family Placodontidae, including the non-armoured forms (*Placodus* and *Paraplacodus*), and Cyamodontidae, including the armoured forms, which in its turn is divided into the subfamilies Cyamodontinae (*Saurosphargis, Cyamodus, Placochelys, Psephosaurus, Psephoderma*) and Henodontinae (*Henodus*).

In 1956, Peyer described a complete skeleton of a reptile found in 1935 at Monte San Giorgio which he regarded as a possible forerunner of placodonts (*Helveticosaurus zollingeri*).

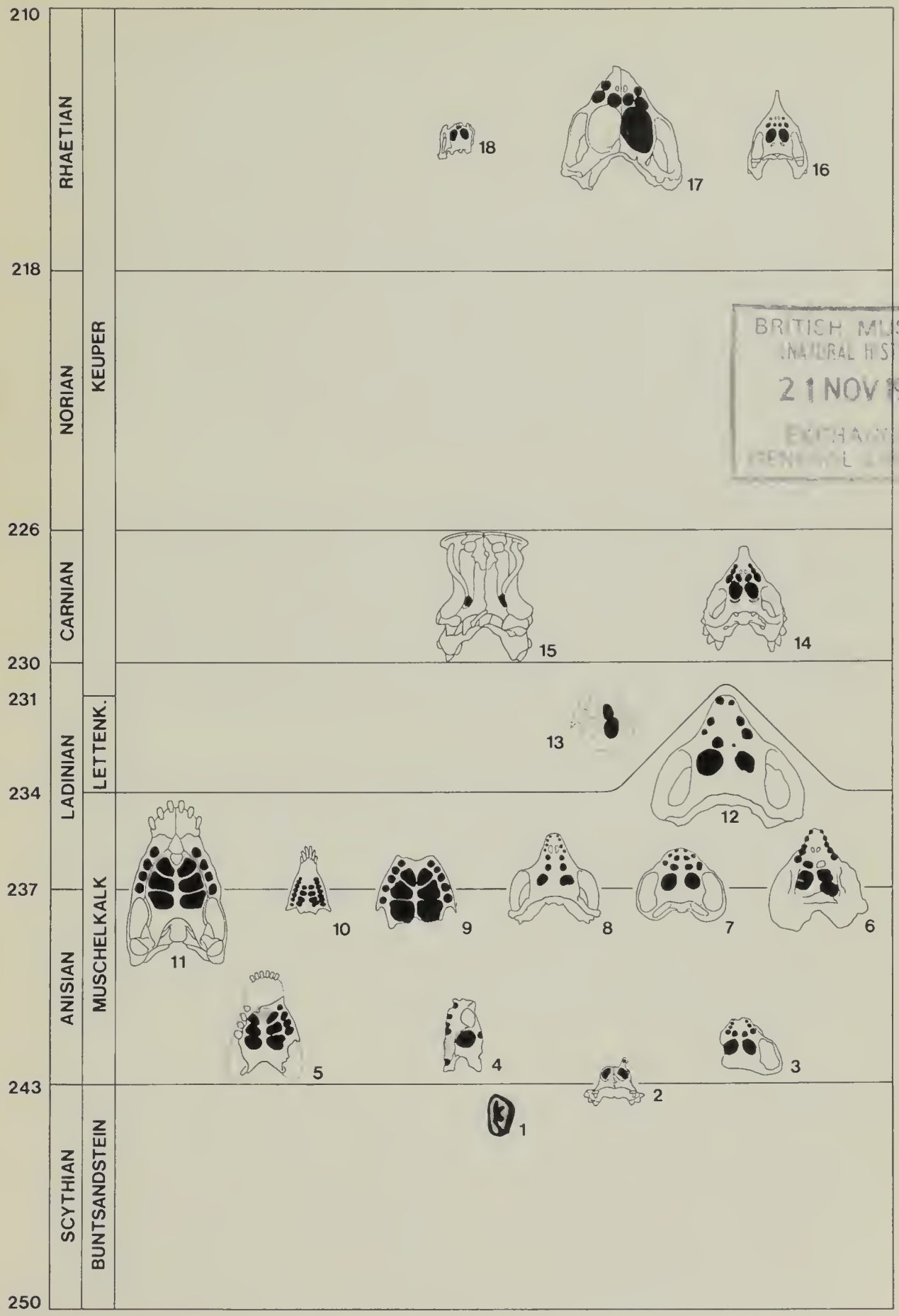
New complete skeletons of armoured placodonts were recently brought to light in Lombardy from Upper Norian rocks (Pinna and Nosotti 1989), and more recently the skull of a new genus was found in the italian Upper Trias (Pinna 1990).

Stratigraphical distribution

On the basis of our present data it appears that placodonts had a very limited distribution in space and time: in fact they lived from the end of the Lower Triassic to the end of the Upper Triassic in western Tethys. They spread both in epicontinental seas – which, especially in the Middle Triassic, covered part of those regions that were more close to Laurasia's and Gondwana's coasts – and in coastal areas of the Tethys sea, characterized by the presence of large carbonatic platforms.

It is not easy to make an exact stratigraphy of placodonts for two reasons: the lack of precise stratigraphical references concerning certain localities and

Figure 1 – Stratigraphical distribution of placodonts. 1 - *Placodus impressus.* 2 - *Psephosaurus mosis.* 3 - *Cyamodus tarnowitzensis.* 4 - *Negevodus ramonensis.* 5 - *Placodus antiquior.* 6 - *Cyamodus hildegardis.* 7 - *Cyamodus münsteri.* 8 - *Cyamodus rostratus.* 9 - *Placodus quinimolaris.* 10 - *Paraplacodus broilii.* 11 - *Placodus gigas.* 12 - *Cyamodus sp.* (Crailsheim spec.). 13 - *Psephosaurus suevicus.* 14 - *Placochelys placodonta.* 15 - *Henodus chelyops.* 16 - *Psephoderma alpinum.* 17 - *Psephoderma raeticus.* 18 - *Psephoderma alpis-sordidae.* Radiometric Scale according to Bilal U. Hag and Frans W. B. van Eyslinga - Geological Time Table, Elsevier 1987.



the absence of sure correlations between deposits belonging to different geographical areas. The biggest difficulties concern the Middle Triassic and they are due to the fact that for this time interval the stratigraphical distribution of placodonts in the German Basin is not very clear. They are also due to the fact that many localities in different countries (Rumania, Turkey, Tunisia) are not precisely dated and that there is not a sure and precise correlation between the European and the Middle Eastern fauna. The only level with an exact stratigraphical position in the Middle Triassic sequence is the Grenzbitumenzone of Monte San Giorgio and Besano, which is placed at the Anisian-Ladinian boundary and which, according to Wild (1972), is more or less contemporary with the placodonts bearing strata of the Bavarian Upper Muschelkalk.

In order to analyse the placodonts' stratigraphic distribution, we referred to the correlations between the German Triassic and the classical subdivisions of Alpine Triassic established by Wild (1980) for the Middle Triassic and by Benton (1986) for the Upper Triassic, while for the Israeli fauna the only stratigraphical reference is still that of Brotzen (1957).

Lower Triassic

The oldest placodont remains were found in the German Basin at a level corresponding to the top of the Lower Triassic (Upper Buntsandstein). There are seven isolated teeth, coming from Zweibruchen (Deux Ponts), on which Agassiz (1839 table 70, fig. 1-7) established the species *Placodus impressus,* and a neural arch found at Sulzbad in Alsace that Huene (1936) ascribed to an unspecified placodont. According to Peyer and Kuhn-Schnyder (1955, page 479) it is possible that not all teeth studied by Agassiz belonged to placodonts, but that at least one of them (table 70, fig. 3) could be ascribed to a representative of the genus *Cyamodus.*

This statement by Peyer and Kuhn-Schnyder is quite interesting: it seems to prove (if Sulzbad's vertebra belonged to a *Placodus*) that since their first appearance placodonts were represented by armoured and non-armoured forms. This makes it impossible to think with absolute certainty that cyamodonts «*are much more derived* (if compared to *Placodus*) *in both dental and skeletal features*», as stated by Peyer and Kuhn-Schnyder (1955) and recently by Sues (1987).

For Lower Triassic there are no additional Placodont remains. The absence of these reptiles from Tethy's marine sediments leads us to believe that these animals did not differentiate before the end of the Lower Triassic and excludes the possibility of a tethyan origin.

Middle Triassic

With the beginning of the Middle Triassic, placodonts become relatively common. At the base of the Lower Muschelkalk, in stratigraphic levels corresponding to the Lower Anisian, they are present in Silesia (Tarnowitz and Gogolin's layers) with the species *Cyamodus tarnowitzensis, Saurospliargis voltzi, Placodus antiquior, Placodus sp., Paraplacodus* sp. (Gürich 1884, Huene 1936), in Germany (Freyburg-s-Unstrut) (Huene 1936) and in the Netherlands (Winterswijk) (Oosterink 1978) with the species *Placodus antiquior,* in Italy with a Cyamodont's vertebra (Trompia Valley's Anisian) (Sacchi Vialli

1956), in Israel (Wadi Ramon) with the species *Negevodus ramonensis* (Mazin 1986) and *Psephosaurus mosis* (Brotzen 1957), the latter at the limit between Lower and Middle Triassic. Therefore at the beginning of the Middle Triassic the two main placodont groups, Cyamodontia and Placodontia, have already differentiated and are widely distributed. But while the formers widespread both in the European epicontinental sea and in the Tethy's coasts, the latter were limited to the Muschelkalk sea of the German Basin.

Placodonts are present at an undetermined level of Anisian in Rumania (Alesd) with poorly definited armoured forms (*Psephosaurus suevicus* (?), *Psephoderma sp., Placochelys aff. placodonta*) and non-armoured forms (*Placodus gracilis* and a form similar to *Paraplacodus broilii*) (Jurcsak 1976, 1977, 1978, 1982). Nevertheless Jurcsak's association of placodonts (1982) is not convincing because it groups together species that, in localities with a well established stratigraphy, are found in different temporal levels; this is probably due to an incorrect classification of the findings.

In the Upper Anisian, in layers probably corresponding to the upper part of the German Lower Muschelkalk, placodonts are present in Sinai (Araif en Naqa) represented by armoured forms (*Psephosaurus sinaiticus*) (Haas 1959).

At the base of the Upper Muschelkalk, placodonts become very abundant in the German Basin; they are the typical Bavarian forms (*Cyamodus rostratus, Cyamodus münsteri, Placodus gigas, Placodus andriani*) coming from a stratigraphic level coeval to the Grenzbitumenzone, corresponding to the limit between the Anisian and the Ladinian. Therefore the Bavarian forms are contemporary with the alpine forms *Cyamodus hildegardis* and *Paraplacodus broilii* (Wild 1972). The complete skeleton of *Placodus gigas* in Senckenberg Museum of Frankfurt was found in Steinsfurt's Lower Hauptmuschelkalk (Heidelberg) which is more or less equivalent to the Upper Anisian-Lower Ladinian.

On the contrary we should ascribe some large German cyamodonts (Crailsheim's «*Cyamodus sp.*») (Kuhn-Schnyder 1959, 1960) and a certain number of *Psephosaurus* from Israel (*Psephosaurus rhombifer, Psephosaurus sp.* Haas 1969) to a higher stratigraphical level, probably corresponding to the top of the Upper Muschelkalk (Upper Hauptmuschelkalk) and therefore to Middle-Lower Ladinian. The placodonts of Tarasci, Turkey, (*Psephosaurus?*) (Beltan et al., 1979) belong to Lower or Middle Ladinian. But we have no certain stratigraphic references for the placodonts of Djebel Rehach, Tunisia, (*Psephosaurus sinaiticus?, Psephosaurus mosis?*) (Gorce 1960, Lehman 1965, Halstead and Stewart 1970). A *Paraplacodus* vertebra found at Henarejos, Spain, can be ascribed to the Upper Ladinian (Pinna 1990).

Psephosaurus picardi, a Wadi Ramon armoured form (Brotzen 1957), must be ascribed to the Upper Ladinian (Mazin 1988).

At this point it is necessary to make a specification about the systematic attribution of the Negev and Sinai forms. These forms, which I could not analyse because of the refusal of Jerusalem's Hebrew University, were superficially studied by Haas (1959, 1967, 1969, 1975) and, more deeply, by Brotzen (1957) and they were ascribed by the two authors to the genus *Psephosaurus* only because their carapace can be approximately compared to that of species described by Fraas. The genus *Psephosaurus* from the german Lower Keuper is a very poorly known form of which we have only badly preserved fragments

of the carapace, some teeth and isolated osteoderms. Probably the Israeli forms have nothing to do with the German *Psephosaurus,* which comes from a younger stratigraphical level. Israeli forms show a big variety of the structure of their carapace (Westphal 1975) and they probably represent different species or even genera. Some fragments of the armour have certain analogies with the carapace of *Cyamodus hildegardis.*

The classification of Middle Triassic cyamodonts isn't simple, because of the fragmentary nature of the material: of the German *Cyamodus* we know only the skulls but not the armour, of the Israeli *Psephosaurus* we know the armour but not the skulls (with the exception of the skull fragment figured by Brotzen in 1957), while of *Cyamodus hildegardis* we know several skulls belonging to individuals of different age and three more or less complete skeletons (Peyer 1931, Pinna 1980 and the non described specimen T.58 of the Zürich Museum). Only a complete revision of the latter species will allow us to clarify the existing relationships among the German, the middle eastern and the alpine forms; they are at least coeval, since they lived in the interval including the Upper Anisian and the Lower Ladinian.

The Middle Triassic ends in the continental area with the Keuper regression. The regions that during Middle Triassic were covered by the Muschelkalk epicontinental seas (European Continental Area, Iberian Peninsula, North Africa) change into land areas. In Germany this transition takes place through a transitional and brackish marine phase named Lettenkeuper, stratigraphically corresponding to the top of Ladinian (Benton 1986). The last placodont of the Middle Triassic, *Psephosaurus suevicus,* comes from these sediments and its rather fragmentary remains were found at Hoheneck, near Ludwigsburg.

Upper Triassic

Placodonts' stratigraphical distribution is clearer in the Upper Triassic than in the previous interval. During the Upper Triassic, placodonts are limited to the coast of the Tethys, because the Keuper regression caused the disappearance of the Muschelkalk epicontinental seas. So the remains of Placodonts can be found only in regions characterized by Alpine Facies Triassic (Southern Calcareous Alps; Austrian and Bavarian Alps, Bakony Forest).

An exception is represented by *Henodus chelyops,* of which several specimens were found in the *Estheria* Schists of Gipskeuper, Middle-Lower Carnian (Vogt 1983, pages 33, 34), of Tübingen-Lustnau. The Gipskeuper represents a lagoonal-brackish episode and therefore *Henodus* is the only known placodont that adapted to a non-marine environment, thus surviving regression. The adaptation to such a particular environment explains the remarkable modifications of this placodont's skull and dentition.

Henodus, whose general anatomical structure is not basically different from that of the other armoured placodonts of the Upper Triassic (*Placochelys placodonta* and *Psephoderma alpinum*), represents in all likelihood a population isolated in an area that was shrunk by the same regression that took place in Continental Europe during the beginning of Upper Triassic.

As already mentioned, placodonts were quite widespread in the Upper Triassic alpine facies. During the whole period exclusively armoured forms

lived on the coasts of the Tethys. They were adapted to life both in the most littoral areas and in the vast shallow carbonatic platforms.

During the Carnian the coastal area of Tethys – where the formation known as Schists of Raibl deposited – were inhabited by *Placochelys placodonta* and *Protenodontosaurus italicus*. Their remains were found at Veszprem (Bakony Mountain), Hungary, in the Lombard Alps (Gorno Formation outcropping at Monte Pora and Colle Vareno) (Nosotti 1986, 1987) and in the Eastern Alps (Raibl Formation outcropping at Dogna and Fusea in Friuli) (Pinna and Zucchi Stolfa 1979; Pinna 1990).

Probably *Protenodontosaurus italicus, Placochelys placodonta* and *Henodus chelyops* were almost contemporary (Peyer and Kuhn-Schnyder 1955): the presence of *Myophoria kefersteini* at the base of Gipskeuper seems to allow a correlation with the Raibl Formation.

During the end of the Upper Triassic (Norian and Rhaetian) placodonts were largely widespread in the coastal areas of western Tethys, which form today the Northern and Southern Calcareous Alps.

Many Norian and Rhaetian species have been described: *Psephoderma alpinum, Psephoderma anglicum, Placochelys malanchinii, Placochelys stoppanii, Placochelys zitteli, Placochelys alpis-sordidae, Macroplacus raeticus,* which nevertheless have many affinities and whose differences are based primarily on differences in size or are due to the incompleteness of the specimens. So it is possible that during this span of time a single species was present: *Psephoderma alpinum.* It is not easy to make an exact stratigraphy of the placodonts for the Norian and Rhaetian. This is due partially to the facies' heteropies linked to the progression of the Rhaetian transgression which sometimes prevent us from making exact chronostratigraphical correlations, and partially to the homogeneity of placodonts, among which it is presently impossible to distinguish different and successive morphological kinds in the chronostratigraphical scale.

As for Placodonts' stratigraphical succession from Upper Norian to Middle Rhaètian, the clearest situation is that of Lombard Alps. Here the only Placodont species *Psephoderma alpinum* was found:

a - in Upper Norian Zorzino Limestone heteropic with Dolomia Principale's top layers,
b - in Riva di Solto Shales of Basal Rhaetian, standing directly above both Zorzino Limestone and Dolomia Principale,
c - in Zu Limestone of Middle Rhaetian, which in its turn lies directly on Riva di Solto Shales.

The Lombardy species *Psephoderma alpinum* is widespread from Upper Norian to Middle Rhaetian and during this interval there are no remarkable modifications. No placodont remains have yet been found in the terminal layers of the Rhaetian of Lombardy, which leads us to think that the extinction of these forms could have taken place just before the end of the Upper Triassic.

Placodonts are present not only in the Lombardy Alps, but also in the Norian of other localities: some isolated teeth, which probably belong to the species *Psephoderma alpinum,* were found in the Austrian Alps (the uppermost part of Mulling Hauptdolomit) (Huene 1956) and in the Bavarian Alps (Plattenkalk of Garmisch-Partenkirchen). It seems that during the Rhaetian

placodonts were confined particularly in the carbonatic platforms. In Lombardy they are present in calacareous-bituminous deposits (Zorzino Limestone), which formed in those basins with restricted water circulation that are present inside the carbonatic platform of Dolomia Principale (Pinna 1987, Pinna and Nosotti 1989). During the Rhaetian, placodonts maintain about the same distribution that characterized them during Upper Norian: they are in fact present in the Lombardy, Bavarian and Austrian Alps. The only known placodont remains outside the alpine area are the armour fragments of the English Rhaetian described by Meyer in 1867 under the name of *Psephoderma anglicum* and some other specimens from the area of Bath, which are presently under study (Duffin personal communication).

The fact that placodonts died out before the end of the Triassic period seems to be confirmed, even though two *Placochelys* teeth were found in the Lower Lias of Arzo, Canton Ticino, Switzerland (Peyer 1931, Peyer and Kuhn-Schnyder 1955): in both cases they are actually reworked teeth, found in the Broccatello d'Arzo, a calcareous breccia containing several fragments of Norian Dolomia Principale and of Rhaetian limestone (Wiedenmayer 1963).

Geographical distribution

The geographical distribution of placodonts has never been throughly studied because of the lack of palaeontological documentation. Mazin (1986) is the only author who tried to make an analysis, even though a brief one, of the geographic distribution of these animals during the Middle Triassic. He states that placodonts (and Nothosauria as well) had a tethyan origin. This means that they appeared in western Tethys, they widespread along Tethys' northern coasts and they finally migrated to the German area during the Middle Triassic, probably in Lower Ladinian, when a connection between the Tethys and the German Basin opened; but this connection was incomplete, since few genera are represented in both areas (only the genus *Psephosaurus* among the twelve known genera of placodonts).

Mazin's hypothesis is dubious if we examine the placodonts' stratigraphy and the geographical distribution of the deposits containing these reptiles.

During the Triassic, in the area of the western Tethys included between the southern border of Laurasia and the northern border of Gondwana, we can generally identify four kinds of sedimentary environments that proceed from the land toward the center of the Tethys (Laubscher and Bernoulli 1977):

1 - continental areas that are subject to local erosion and continental sedimentation,
2 - areas that are occasionally subject to marine invasions with formation of epicontinental seas,
3 - highly subsiding areas characterized by accumulation of large carbonatic platform,
4 - areas that are characterized by sediments from a deeper sea.

Placodonts remains were found in the second and in the third environment which correspond respectively to German Facies' Triassic and Alpine Triassic; they were also found in some transition areas.

The distribution of the placodonts in the Triassic period was influenced by these general geographical conditions of the Tethys' western area and particularly by the succession of transgressions and regressions and by the opening and closing of connections between the Tethys and the epicontinental seas.

As already seen, the oldest placodonts appeared at the top of the Lower Triassic in the German area, already differentiated in armoured and non-armoured forms.

Since no placodont remain has been found in Tethys' marine sediments of the Lower Triassic, and since from most of the Middle Triassic the Tethys contained just the armoured forms, it is possible to believe that placodonts originated from the european epicontinental basins. They probably originated from a group of land reptiles, because of the selective pressure of the epicontinental seas' advance which took place at the end of the Lower Triassic. At the beginning of the Middle Triassic placodonts were widespread in all epicontinental seas of the Muschelkalk (Central-western Europe, Iberian Peninsula, North Africa) and in the carbonatic platforms of Tethys' northern coasts (Lombardy Alps, Turkey, Rumania) and southern coasts (Israel, Sinai). During this whole period there are both armoured forms (*Placodus* and *Paraplacodus*) and non-armoured forms (*Saurosphargis* and *Cyamodus*) in the epicontinental seas, while in Tethys there are only the armoured forms; the latter are different from those characterizing European epicontinental seas (middle-eastern *Psephosaurus*). During all the Middle Triassic placodont faunas of the epicontinental seas and of the Tethys' coastal carbonatic platforms are rather distinct; an exception were the border areas like Transylvania which, during the Anisian, represented «*an intermediate spot toward Silesia's door*» (Jurcsack 1982). Here were found, together with Tethyan forms (whose classification must be revised), some remains of *Placodus* and *Paraplacodus*. The genera *Placodus* and *Cyamodus s. str.,* for instance, are never found in the Tethyan area, while *Psephosaurus suevicus* seems to have no relationships with the other middle-eastern «*Psephosaurus*».

There was a greater exchange between the two areas during the passage between Anisian and Ladinian (Grenzbitumenzone), when «European» Cyamodonts (*Cyamodus hildegardis*) and non-armoured forms (*Paraplacodus*) appear in the tethyan area.

At the beginning of the Upper Triassic the placodonts' area of distribution shrinks at the same time as the Lower Keuper regression. During most of the Upper Triassic, placodonts are limited to Tethys' coastal platforms, with the exception of the genus *Henodus,* which adapted to lagoonal-brackish conditions in a small area of the German Basin.

The Rhaetian transgression did not cause a new spread of placodonts, but the only known Rhaetian genus, *Psephoderma,* expanded its area up to the British Islands.

Just before the end of the Upper Triassic, placodonts died out. Halstead (1967) correlated the extinction of placodonts with the appearance (and related competition) of durofagous holosteans and with the development of those Batoidea which were adapted to a durofagous diet: placodonts could not compete with these two groups because they were air breathing animals.

It is very unlikely that the extinction of placodonts was caused by compe-

tition (Pinna and Nosotti 1989). On the contrary it was probably caused by environmental changes linked to the rifting of the western Tethys, which influenced extremely specialized forms.

At the end of the Triassic, the Tethys' breakup caused the submersion of shallow marginal platforms, thus causing the disappearance of the environment to which armoured placodonts of the Upper Triassic (*Psephoderma alpinum* and related forms) were adapted.

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